

A SURVEY OF SEED COAT MORPHOLOGY IN OXYTROPIS, SECTS.
ARCTOBIA, BAICALIA, GLAEOCEPHALA, MESOGAEA,
AND OROBIA (FABACEAE) FROM ALASKA

Zachary J. Meyers

University of Alaska Museum of the North
907 Yukon Drive
Fairbanks, Alaska 99775, U.S.A.
zjmeyers@alaska.edu

Stefanie M. Ickert-Bond¹

University of Alaska Museum of the North
907 Yukon Drive
Fairbanks, Alaska 99775, U.S.A.
smickertbond@alaska.edu ¹ Author for correspondence

Rose LaMesjerant

University of Alaska Museum of the North
907 Yukon Drive
Fairbanks, Alaska 99775, U.S.A

ABSTRACT

Seed coat micromorphology for 22 of 67 species of the genus *Oxytropis* from the Arctic in sections *Arctobia* (nine species), *Baicalia* (two species), *Glaeocephala* (three species), *Mesogaea* (one species), and *Orobia* (seven species) were studied using Scanning Electron Microscopy (SEM). Three main types of seed coat micromorphology (i.e., rugulate, lophate, and foveolate) and four distinct seed shapes (i.e., reniform, mitiform, globose, and ovoid) were found. Seed coat variation was examined using multinomial regression analysis of taxonomic classification, seed dimensions and geographical distribution. The relative frequency of the seed coat types and seed shape compared to sectional classification showed section *Mesogaea* to be differentiated from sections *Arctobia*, *Baicalia*, *Glaeocephala*, and *Orobia*. *Oxytropis deflexa* of section *Mesogaea* is unique among the taxa studied in having small, globose seeds when compared with the other Alaskan taxa with larger, reniform seeds. Overall, seed micromorphology among the Alaskan members of *Oxytropis* is highly variable at the species level, with some species (i.e., *O. viscida* and *O. jordalii*) demonstrating all three seed coat types.

RESUMEN

Se estudió la micromorfología de la testa de 22 de las 67 especies del género *Oxytropis* del Ártico de las secciones *Arctobia* (nueve especies), *Baicalia* (dos especies), *Glaeocephala* (tres especies), *Mesogaea* (una especie), y *Orobia* (siete especies) fueron estudiadas por Microscopía Electrónica de Barrido (SEM). Hay tres tipos principales de micromorfología de la testa (i.e., rugulada, lofada y foveolada) y se encontraron cuatro formas distintas de semillas (ej., reniformes, mitiformes, globosas y ovoides). La variación de la testa se examinó mediante un análisis de regresión multinomial de la clasificación taxonómica, las dimensiones de semillas y la distribución geográfica. La frecuencia relativa de los tipos de semillas de la capa y forma de la semilla en comparación con la clasificación seccional mostró que la sección *Mesogaea* debe diferenciarse de las secciones *Arctobia*, *Baicalia*, *Glaeocephala* y *Orobia*. *Oxytropis deflexa* de la sección *Mesogaea* es único taxon estudiado que tiene semillas pequeñas, globosas, en comparación con los otros grupos taxonómicos de Alaska con semillas grandes, reniformes. En general, la micromorfología de la semilla entre los miembros de Alaska de *Oxytropis* es muy variable a nivel de especie, con algunas especies (por ejemplo, *O. viscida* y *O. jordalii*) que demuestran los tres tipos de cubierta en las semillas.

INTRODUCTION

The genus *Oxytropis* DC. (Fabaceae, subfamily Papilionoideae, tribe Galegeae Dumort.) is taxonomically complex, comprising over 300 species worldwide (Yakovlev et al. 1996; Yurtsev 1999; Zhu & Ohashi 2000; Welsh 2001; Lewis et al. 2005). The genus is widely distributed throughout the Northern Hemisphere, with its greatest diversity found in the Tibetan plateau and circumpolar Arctic (Yurtsev 1999; Ranjbar et al. 2009). A total of 67 species are found in the Arctic, 22 of which occur in Alaska (Yurtsev 1999; Elven & Murray 2011). *Oxytropis* is thought to have derived from *Astragalus* L. approximately 12–16 Ma and consequently shares many morphological characteristics (Wojciechowski et al. 2005). A beaked keel, asymmetrical leaflets, and an acaulescent habit distinguish *Oxytropis* from *Astragalus* morphologically (Barneby 1952). Many of the taxonomic relationships within *Oxytropis* remain problematic, likely due to relatively recent diversification (reviewed in Welsh 2001).

Several times in the Quaternary during glacial maxima an ice-free, continuous land bridge extended from the Russian Far East to Alaska and Canada and played a significant role in the history of many northern taxa (Hultén 1937, 1958; Elias et al. 1996; Ickert-Bond et al. 2009). In fact, a large ice-free refugium existed from the northwestern-most Arctic in Canada to the Lena River in arctic Russia, the area defined and named Beringia by Hultén (1937). *Oxytropis* present in Beringia, range in distribution from amphi-Beringian taxa to groups endemic to eastern (Alaskan) or western (Russian) Beringia to circumpolar elements, some with extensions southward into the Rocky Mountains (Yurtsev 1997, 1999; Talbot et al. 1999; Ickert-Bond et al. 2009). The suspected recent diversification of the genus coupled with specialized niches (i.e., *O. kobukensis* S.L. Welsh, *O. kokrinensis* A.E. Pors., and *O. tananensis* Jurtz.) has resulted in high levels of intraspecific morphological variation and phenotypic plasticity. In addition, the lack of definitive taxonomic characters in some complexes, have led to difficulties and differences in species delimitation, resulting in competing taxonomies and a plethora of synonyms (reviewed in Welsh 2001).

Alexander Bunge's worldwide treatment of *Oxytropis* (1874) established four subgenera based on the presence and variation of a septum in the legume fruit and the length of the calyx teeth: I. *Oxytropis* (pod exerted above the calyx, with pod always ventrally and sometimes also dorsally septate), II. *Phacoxytropis* (pod exerted above torn calyx, without septum), III. *Physoxytropis* (small, somewhat inflated legume enclosed by intact calyx), and IV. *Ptiloxytropis* (small pods enclosed by calyx with long villous calyx teeth). Bunge (1874) furthermore distinguished 17 sections within *Oxytropis* based on leaflet arrangement, raceme size and shape, legume shape and anatomy, presence of glandular hairs, and presence of spines on the petiole. Many of Bunge's infrageneric categories are still used in taxonomic works today (Barneby 1952; Yurtsev 1997, 1999; Zhu & Ohashi 2000; Polozhij & Malyshev 2006; Malyshev 2008a, 2008b; Ranjbar et al. 2009).

Revisionary work on members of *Oxytropis* was completed by Vasil'chenko (1948), who added two subgenera exclusively of Old World taxa. In 1952 Barneby revised *Oxytropis* for North America, clarifying much of the nomenclatural issues that had arisen. Yurtsev (1997, 1999) treated the genus from a Panarctic perspective and noted the importance of substrate affinity to the distribution of certain taxa. Most recently, Welsh (2001) revised *Oxytropis* in North America, largely agreeing with the species concepts proposed by Barneby. These authors placed importance on characters such as stipule shape, pubescence type, legume shape, and substrate affinity to delineate taxa. Although the Panarctic Flora Checklist provides a unified view for all areas of the Arctic (<http://nhm2.uio.no/paf>), the high phenotypic plasticity observed in some taxa along with differences in species concepts between Russian and American taxonomists result in no widely accepted taxonomy for the group.

The varied climates, lithologies, and landforms (many created and modified by cold climate geomorphic processes) in Alaska generate a number of different habitats and ecological niches. Steep gradients of abiotic factors such as disturbance, elevation, and moisture result in sharply contrasting adjacent habitats. Thus weak geographic and ecological reproductive isolation among rapidly diversifying taxa might well have allowed intraspecific and interspecific hybridization in *Oxytropis* (Jorgensen et al. 2003; Artyukova & Kozyrenko 2012). These phenomena often caused by the influx of multiple rapid colonization events have occurred in a number of arctic genera including, *Artemisia*, *Cassiope*, and *Rubus* (Eidesen et al. 2007; Ehrich et al. 2008; Tkach et al. 2008).

The few morphologic and phylogenetic studies that have been conducted in *Oxytropis* have yet to yield an accepted unified taxonomy for the genus. Jorgensen et al. (2003) using ITS and RAPD markers for populations of *O. campestris* and *O. arctica* complexes in Alaska suggested that the taxa examined represent a recent radiation and are the result of multiple origins of polyploidy. Most recently, a phylogenetic study based on ITS sequence data from 35 species revealed largely unresolved relationships of the genus (Archambault and Stromvik 2012). However, the 2012 study substantiates some infrageneric relationships within the genus, namely the identification of section *Mesogaea* as the first branching lineage of *Oxytropis*, as well as multiple recent radiation events of *Oxytropis* in the Arctic.

Within Fabaceae several studies have investigated the value of seed coat micromorphological characters

as seen with SEM for identifying economically important taxa (Lersten 1981; Pandey & Jha 1988). Forty-eight species of Turkish *Astragalus* were examined (Vural et al. 2008) investigating seed micromorphology, the study revealed two distinct seed coat types (i.e., rugulate and rugulate-reticulate, terms consistent with those used in our study) and three distinct seed shapes (i.e., peroblate, suboblate, and oblate). Seed shapes were taxonomically useful only when combined with seed coat patterns in Turkish and Iranian *Astragalus* (Vural et al. 2008; Ranjbar 2009). Seed coat patterns in *Oxytropis* have been documented as rugulate, lophate, or multi-reticulate. However, only a few species have been examined (i.e., *Oxytropis riparia* Litv., *Oxytropis campestris* Hook., *Oxytropis lambertii* Pursh), and none from Alaska (Lersten 1981; Pandey & Jha 1988; Solum & Lockerman 1991). Recently Erkul and Aytac (2010) examined 13 Turkish species of *Oxytropis* and classified seed coats as striate-reticulate, psilate-reticulate, reticulate, and striate-rugulate.

In the current paper, we extended the SEM survey of seed coat micromorphology, shape and size into the Alaskan *Oxytropis*. In order to test the value of seed coat micromorphology we examined representatives of sections *Arctobia*, *Baicalia*, *Glaeocephala*, *Mesogaea*, and *Orobia*. Multinomial logistic regression analysis was employed for several independent variables (taxonomic classification, seed dimensions, and geographical distribution) to describe seed coat variability.

MATERIALS AND METHODS

Our survey of seed coat micromorphology of *Oxytropis* included 22 Alaskan taxa of the 67 arctic species that have been described (Yurtsev 1999; Elven & Murray 2011; Table 1). Most of the remaining arctic species are from the Old World (e.g., the Russian Far East, Siberia, and Scandinavia). Within the 22 Alaskan *Oxytropis*, we included nine species from sect. *Arctobia* (of 13 classified in this section), two from sect. *Baicalia* (of eight classified in this section), three from sect. *Glaeocephala* (of 13 classified in this section), one of sect. *Mesogaea* (of three classified in this section), and seven from sect. *Orobia* (of 27 classified in this section; Table 1). For four species in sect. *Arctobia* (*O. arctobia* Bunge, *O. bryophila* (Greene) Jurtz. subsp. *lonchopoda* (Barneby) Cody, *O. czukotica* Jurtz., and *O. mertensiana* Turcz.), we included additional samples that were collected from neighboring regions on the Chukotka or Kamchatka peninsulas (Russia) and the Yukon Territory (Canada).

Our study is based primarily on mature, fully expanded seeds that were removed from herbarium specimens; several immature, flattened or partially broken seeds were also examined, when insufficient material was available (Table 1). Seeds were soaked in 90% ethanol for 24 hours and air-dried. For anatomical study, seeds were soaked in a mixture of equal parts water, glycerol, and ethyl alcohol for 30 hours and samples were then hand sectioned with a razor blade. Seed anatomy was examined from representatives of each taxonomic section. For Scanning Electron Microscopy (SEM) whole and sectioned seeds were mounted on SEM stubs with double-sided tape, sputter-coated with a palladium target (60/40) in a Ladd model, and viewed with an ISI-SR-50 SEM at 15–20 kV at the Advanced Instrumentation Laboratory (AIL), University of Alaska Fairbanks. Following Lersten (1981), seed coat micromorphology was examined in regions adjacent to the hilum at magnifications ranging from 500–2000 \times .

Measurements of seed length (L) and width (W) were made with an ocular micrometer on a stereoscopic microscope as well as from the SEM image file with a scale bar at 30–50 \times . Measurements given are the mean length (measured transversely to the hilum) and width (measured longitudinally to the hilum) in millimeters (Table 1). A minimum of three specimens per taxon were examined; for every specimen three seeds were measured. Terminology used for seed shapes and seed coats follow Lersten (1981) and Barthlott (1990).

Statistical analyses.—We compared the relative frequency of seed coat types (i.e., rugulate, lophate, foveolate) with respect to taxonomic sections, species, seed length, seed width, latitude, and longitude to evaluate taxonomic, physiological, and geographical correlations. Multinomial logistical regression was performed in R version 2.10.0 (R Development Core Team 2009) using the library (Venables & Ripley 2002) with the objective of testing potential predictive variables of seed coat type. Delimitation of taxonomic section, species, latitude, longitude, seed length, and seed length-to-width ratio (L:W) were used as independent variables (IVs) in the model, with seed coat type as the dependent variable (DV). We used an information theoretical approach

TABLE 1. Specimens examined along with voucher information and locality data. * All vouchers examined are deposited at the University of Alaska Museum of the North Herbarium (ALA) (unless otherwise noted). Herbarium acronyms follow Index Herbariorum (Thiers 2008). † denotes irregular or partially broken seeds. Surface ornamentation is categorized in five types: rugulate (R), rugulate reticulate (RR), multi-reticulate (MR), lophate (L), and lophate reticulate (LR). Latitude, longitude are recorded below (Index of Plant Chromosome Numbers, IPCN).

Species	Locality	Voucher information*	Mean Length (mm)	Mean Width (mm)	Seed Shape	Surface Ornament.	Lat. (°)	Long. (°)
Oxytropis subgen. Oxytropis sect. Arctobia								
<i>O. arctobia</i>	Canada: Southampton Island	Malte 119782	1.12	1.46	reniform	R, RR	64.10	-82.50
<i>O. arctobia</i>	Canada: Banks Island	Aiken 99-015 (CAN)	1.89	2.34	reniform	R, RR	73.22	-119.53
<i>O. arctobia</i>	Canada: Spence Bay.	McGrath s.n. (CAN)	1.46	1.64	reniform to mitiform	R, RR	69.53	-93.53
<i>O. bryophila</i>	Seward Peninsula	Murray, Yurtsev & Kelso 10658	2.05	1.77	reniform (†)	R, RR	65.69	-164.39
<i>O. bryophila</i>	Alaska Peninsula	Jansen & Carlson 02-127	2.05	2.2	reniform to mitiform	R, RR	58.61	-153.77
<i>O. bryophila</i>	Mt. Schwatka	Parker et al. 4949	1.44	1.99	reniform (†)	R, RR	65.88	-147.25
<i>O. bryophila</i>	Chugach Mts., Knik River	Barker 02-217	1.85	2.22	reniform to mitiform	R, RR	61.36	-148.91
<i>O. bryophila</i>	Nulato Hills, Debauch Mtn.	Parker et al. 7256	1.5	2.09	reniform	R, RR	64.51	-159.88
<i>O. bryophila</i>	Twelvemile Summit	Ickert-Bond 1526	1.63	1.95	mitiform	R, RR	65.39	-145.97
<i>O. bryophila</i> subsp. <i>lonchopoda</i>	Canada: Ogilvie Mts.	Cody & Ginns 34315	1.77	2.03	reniform	R, RR	65.29	-140.30
<i>O. czukotica</i>	Russia: Kamchatka	Kharkevich 550a	1.2	1.63	reniform	L, LR	62.35	168.90
<i>O. czukotica</i>	Russia: E Siberia	Koroleva & Petrovsky s.n.	2.28	1.82	mitiform	R, RR, MR	69.58	164.41
<i>O. gorodkovii</i> Jurtz.	Seward Peninsula, Minnie Creek	Murray, Yurtsev & Kelso 11565	1.67	1.85	reniform	R, RR	65.33	-163.63
<i>O. gorodkovii</i>	Ogotoruk Cr. drainage	Hultén s.n.	2.17	2.17	mitiform	R, RR	68.13	-165.66
<i>O. gorodkovii</i>	Seward Peninsula, Lost R. Drainage	Lenarz 46	1.86	2.25	reniform to mitiform	RR	65.45	-167.15
<i>O. huddelsonii</i> A.E. Pors.	Yukon-Tanana Upland, Yukon Fork	Parker et al. 6511	1.99	2.61	reniform to mitiform	R, RR	65.15	-143.70
<i>O. huddelsonii</i>	Chugach Mts., Granite Range, E of Goat Cr.	Batten & Barker 96-321	1.89	1.94	reniform to mitiform	L, RR	60.99	-142.01
<i>O. huddelsonii</i>	Yukon-Tanana Upland, Charley River	Roland 5713	1.47	1.99	mitiform	R, RR	64.61	-143.68
<i>O. huddelsonii</i>	Alaska Range, Clearwater Mts.	Grundt s.n.	2.21	2.36	reniform to mitiform	R, LR	63.03	-147.20
<i>O. huddelsonii</i>	Wrangel St. Elias N.P., Nicolai Ridge	Ickert-Bond 1640	1.88	2.21	mitiform	R	61.45	-142.65
<i>O. kokrinensis</i>	Vicinity of Akilik River	Duffy MD07-105	2.2	2.71	mitiform	R, RR	67.33	-159.96
<i>O. kokrinensis</i>	Etvluk Test Well	Murray 6889	1.5	1.43	reniform	RR	68.36	-156.75
<i>O. kokrinensis</i>	Brooks Range, Bornite	Lewis s.n.	1.6	1.5	mitiform	RR	67.08	-156.91
<i>O. mertensiana</i>	Brooks Range, Mi 271 Dalton Hwy.	Murray 8541	1.93	1.77	mitiform	R, RR	68.45	-149.30
<i>O. mertensiana</i>	Brooks Range, Carnivore Cr.	Batten 856	1.18	1.25	reniform	R, RR	69.28	-145.03
<i>O. mertensiana</i>	Russia: Chukotka, Getlyan River	Razzhivin et al. s.n.	1.95	1.92	mitiform	R, RR	65.25	172.16
<i>O. scammaniana</i> Hult.	Wrangel St. Elias N.P., Nicolai Ridge	Ickert-Bond 1638	1.31	1.82	reniform	R, RR	61.46	-142.64
<i>O. scammaniana</i>	Etvluk Test Well	Murray 6890	1.5	1.7	reniform (†)	R, RR	68.36	-156.75
<i>O. scammaniana</i>	Ptarmigan Heart	Raup, Raup, & Drury Jr. 13739	1.3	1.33	reniform to globose (†)	R, RR	61.81	-138.58

TABLE 1. Specimens examined along with voucher information and locality data. * (continued)

Species	Locality	Voucher information*	Mean Length (mm)	Mean Width (mm)	Seed Shape	Surface Ornament.	Lat. (°)	Long. (°)
sect. <i>Baicalia</i>								
<i>O. splendens</i> Douglas	Eagle Creek Campground	Ickert-Bond 1568	1.67	1.7	reniform	L	63.16	-143.20
<i>O. splendens</i>	Road to Chitina, W of Tosina River	Galen Smith 2342	1.78	1.69	reniform to mitiform	L, R	61.65	-144.65
<i>O. splendens</i>	Yukon River at mouth of Woodchopper Cr.	Parker & Batten 6218	2.63	2.51	mitiform	L, LR	65.36	-143.35
<i>O. tananensis</i>	Canada: Yukon Territory, Carmacks	Calder & Kukkonen 27976	1.5	1.63	ovoid †	RR	62.11	-136.26
<i>O. tananensis</i>	Porcupine River	Howenstein & Borron 40	2.24	3.01	mitiform to ovoid	L, LR	67.40	-141.08
<i>O. tananensis</i>	Yukon-Tanana Upland Gaffney Road	Duffy 95-710	1.46	1.49	mitiform to ovoid	L, LR, F	64.83	-147.64
sect. <i>Glaeocephala</i>								
<i>O. borealis</i> Trautv. ex C.A. Mey.	Seward Peninsula, Salmon Lake	Murray, Yurtzev, & Kelso 10984	0.92	1.4	reniform	R, RR, LR	64.91	-164.95
<i>O. borealis</i>	Killik River valley, Ivisak Creek	Parker et al. 13030	1.58	2.01	reniform (†)	LR, MR	68.30	-154.05
<i>O. borealis</i>	Central Noatak R. valley, Sisiak Creek	Parker et al. 15056	1.22	1.71	reniform to mitiform	RR	68.00	-161.41
<i>O. glutinosa</i> A.E. Pors.	Mackenzie Delta's East Channel	Sim 6092	1.37	2.06	mitiform	RR, L	60.677	-134.129
<i>O. glutinosa</i>	Alaska Range, Tonzona River	Viereck 5368	2.1	2.45	reniform to mitiform	R, RR	62.83	-152.33
<i>O. viscida</i> Nutt.	Canada: Yukon Territory, vic. Burwash Landing	Raup, Drury, & Raup 13962	1.74	1.76	mitiform	RR, MR, F	61.36	-138.98
<i>O. viscida</i>	Akmalik Creek	Parker 7618	1.9	2.04	mitiform to ovoid	L, LR	68.40	-154.15
<i>O. viscida</i>	Canada: Yukon Territory, Kluane Lake	Raup & Raup 12908	1.57	1.70	reniform	RR	61.55	-138.66
sect. <i>Orobia</i>								
<i>O. arctica</i> R. Br.	Seward Peninsula, Mystery Creek	Murray, Yurtzev, & Kelso 11640	1.79	2.17	reniform to mitiform	LR, RR	65.91	-163.5
<i>O. arctica</i>	Arctic Coastal Plain, Sagavanirktok River	Jorgensen & Batten JJ-9-9-9-7	1.18	1.67	reniform	LR, RR	69.56	-148.61
<i>O. arctica</i> var. <i>barnebyana</i> S.L. Welsh	Baird Mts., Squirrel R., 'No Name Cr.'	Jorgensen et al. JJ-97-11-3	1.42	1.98	reniform to mitiform	L, RR	67.44	-161.32
<i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., Squirrel R., 'No Name Cr.'	Jorgensen, et al. JJ-97-16-3	2.07	2.72	reniform to mitiform	L, LR	67.44	-161.32
<i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., Squirrel R., 'No Name Cr.'	Jorgensen, et al. JJ-97-13-2	1.77	2.66	reniform to mitiform	L, RR	67.44	-161.32
<i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., North Fork Squirrel R.	Jorgensen, et al. JJ-97-10-1	1.81	2.46	mitiform	L	67.49	-161.01
<i>O. campestris</i>	Dall Island, Grace Mtn. vic.	Stensvold 5563	1.67	1.86	reniform to mitiform (†)	R, L, LR	54.91	-132.95
subsp. <i>gracilis</i> (A. Nelson) Hult.	Northway, Tetlin NWR bunkhouse	Moran 155	1.42	1.92	mitiform	L, LR	62.96	-141.93
<i>O. campestris</i> subsp. <i>gracilis</i>	Brooks Range, Mile 180 Dalton Hwy	Jorgensen & Batten s.n.	1.92	2.28	reniform to mitiform	R, RR, L	67.31	-150.15
<i>O. campestris</i> subsp. <i>gracilis</i>	Alexander Archipelago	Calhoun & Kriekhaus 63	1.35	1.84	mitiform	MR, F	57.73	-136.06
<i>O. jordalii</i> A.E. Pors.	Kenai Peninsula, Upper Nuka R. valley	Lipkin & Carlson 03-310	1.38	1.65	reniform to mitiform to ovoid	LR, F	59.673	-150.69

TABLE 1. Specimens examined along with voucher information and locality data. * (continued)

Species	Locality	Voucher information*	Mean Length (mm)	Mean Width (mm)	Seed Shape	Surface Ornament.	Lat. (°)	Long. (°)
<i>O. jordalii</i>	Mesa Archaeological Site	Jorgensen & Batten s.n.	1.18	1.55	reniform	L, R	68.41	-155.8
<i>O. jordalii</i>	Brooks Range, Mi 271 Dalton Hwy.	Jorgensen & Batten JJ-99-10-11	1.01	0.87	ovoid to globose	L	68.44	-149.35
<i>O. jordalii</i>	Central Nigu R. valley	Parker 7562	1.78	2.09	mitiform to ovoid	L	68.33	-156.4
<i>O. kobukensis</i>	Kobuk Valley Nat. Park, Kobuk Dunes	Duffy MD07-123	1.82	2.55	mitiform to ovoid	L, LR	67.03	-158.76
<i>O. kobukensis</i>	Kobuk Valley Nat. Park, Kobuk Dunes	Duffy MD07-119	1.9	2.63	mitiform to ovoid	L, RR, R	67.03	-158.77
<i>O. kobukensis</i>	Kobuk R. valley, Paungaq Taugruk	Lipkin 84-47	1.74	1.94	reniform to mitiform	L, LR	67.18	-158.5
<i>O. koyukukensis</i> A.E. Pors.	Brooks Range, Mile 187.2 Dalton Hwy	Jorgensen & Batten JJ-99-11-12	1.67	1.87	mitiform	LR, L, RR	67.45	-150.13
<i>O. koyukukensis</i>	Brooks Range, Mile 187. 2 Dalton Hwy	Jorgensen & Batten JJ-99-11-7	1.54	1.7	globose (†)	F, RR	67.45	-150.13
<i>O. koyukukensis</i>	Noatak River, N of Twelvemile Creek	Peter Ray N.06-10	1.51	1.43	mitiform	R, RR	65.40	-145.91
<i>O. maydelliana</i> Trautv.	Seward Peninsula, VABM Bluff	Kildaw s.n.	2.45	2.4	reniform to mitiform	LR, RR	64.53	-163.75
<i>O. maydelliana</i>	Eagle Summit	Ickert-Bond 1549	1.53	1.77	reniform	R, RR	65.48	-145.40
<i>Oxytropis</i> subgen. <i>Phacoxytropis</i> sect. <i>Mesogaea</i>								
<i>O. deflexa</i>	Wrangel St. Elias N.P., Jack Creek	Ickert-Bond 1595	1.44	1.45	globose	L, LR	62.46	-143.10
<i>O. deflexa</i>	Central Noatak R. valley, Sisiak Creek	Parker et al. 15052	1.38	1.35	globose	R, L	68.00	-161.41
<i>O. deflexa</i>	Dalton Highway, station 5	Ickert-Bond 1466	1.08	1.25	globose	L, LR	67.05	-150.32

TABLE 2. Summary statistics of the multinomial logistic regression with AIC model selection of seed coat micromorphology. Delimitation of taxonomic section (referred to in table as "section"), species, latitude, longitude, length and length to width ratio. The data partition examines three primary seed coat types (i.e. rugulate, lophate, foveolate).

Independent Variables Selected	AIC Score
Section+Species+Latitude+Longitude+Length+L:WW	241.1210
Section+Latitude+Longitude+Length+L:W	231.4239
Section+Latitude+Length+L:W	228.8970
Section+Length+L:W	228.4271
Section+Length	232.7890
Section	234.1854

to select the most parsimonious model of all candidates by minimizing Akaike's information criterion (AIC) to determine which independent variables explain variation of seed coat type (Table 2, Akaike 1974). AIC was implemented as a relative measure for goodness of fit, which penalizes the number of parameters in the model to prevent overfitting (Akaike 1974).

RESULTS

Seed coat types and shapes.—The morphological characteristics of the seeds are summarized in Table 1. All seeds examined appear smooth under the dissecting scope and show a uniform dark to light brown pigmentation (Fig. 1). Typically the seeds are reniform, but when the lobes are unequal in lengths they are classified as mitiform *sensu* Murley (1951) (Fig. 1C–D). Fewer seeds are ovoid or globose as defined by the length-to-width ratio (Table 1; Fig. 1A–B). Seeds of *Oxytropis* examined in this study range from 0.87 mm to 2.9 mm in width and from 1.0 mm to 2.1 mm in length, with an average length-to-width (L:W) ratio of 0.874:1 (Table 1).

Seed anatomy.—The cross-sections revealed the seed coat in all specimens to be well differentiated and exotestal with the outer integument providing the mechanical layer of the seed coat (Fig. 3A). A uniseriate epidermis is covered by a cuticle on upper anticlinal walls (Fig. 3A–C), and is composed of prominent macro-sclereids (Figs. 1B–C), followed by a single row of osteosclereids (hypodermis) and five to eight rows of compressed, tangentially elongate parenchyma cells of the nucellus (Fig. 3C).

Micromorphology.—Three primary seed coat types (i.e., rugulate, lophate, and foveolate) were observed with many species (i.e., *Oxytropis arctica* var. *barnebyana*) exhibiting multiple cuticular patterns among different individuals (Fig. 5). The majority of seeds (63%) in these 22 *Oxytropis* species show a rugulate seed coat characterized with irregularly roughened cuticular folds (R=rugulate, Fig. 2A–D, Table 1). Within rugulate seed coats we recognized a multi-reticulate form (MR), which consist of a secondary mesh of interlacing ridges and irregularly roughened cuticular folds and were found in 50% of the rugulate seeds examined (Fig. 2C–D, Table 1). Approximately 32% of the seeds examined demonstrated the lophate seed coat type, which consists of distinct short ridges with irregular sides forming uplifted circular or rectangular patterns (L= lophate, Fig. 2G–I, Table 1). We observed additional reticulation of the lophate type on a few specimens and recognized those as lophate-reticulate (LR, Fig. 2G, Table 1). The cuticular ridges on the lophate-reticulate pattern are relatively thin when compared to the ridges in multi-reticulate seed coats. The foveolate seed coat type characterized by irregular circular folds with blunt edges and thick cell walls raised above the seed surface were only observed on 5% of seeds examined (F= foveolate, Fig. 2E–F, Table 1). The foveolate type (Fig. 2E–F, Table 1) was found in only four species (i.e., *O. tananensis*, *O. jordalii*, *O. koyukensis*, and *O. viscida*).

Statistical Analysis.—Stepwise model selection of the multinomial logistic regression for the three major classes of seed coat types showed the strongest association with sectional classification, length of seed (size), and L:W ratio (shape). These factors produced the most parsimonious and descriptive model with an AIC score of 228.42 (Table 2). Seed coat type was associated with taxonomic sectional classification, since the removal of this factor increased the AIC score ($\Delta\text{AIC} = +10.23$), indicating its significance to the overall variation observed. Two of the five sections differed in seed morphology; section *Mesogaea* had a uniquely globose seed shape and

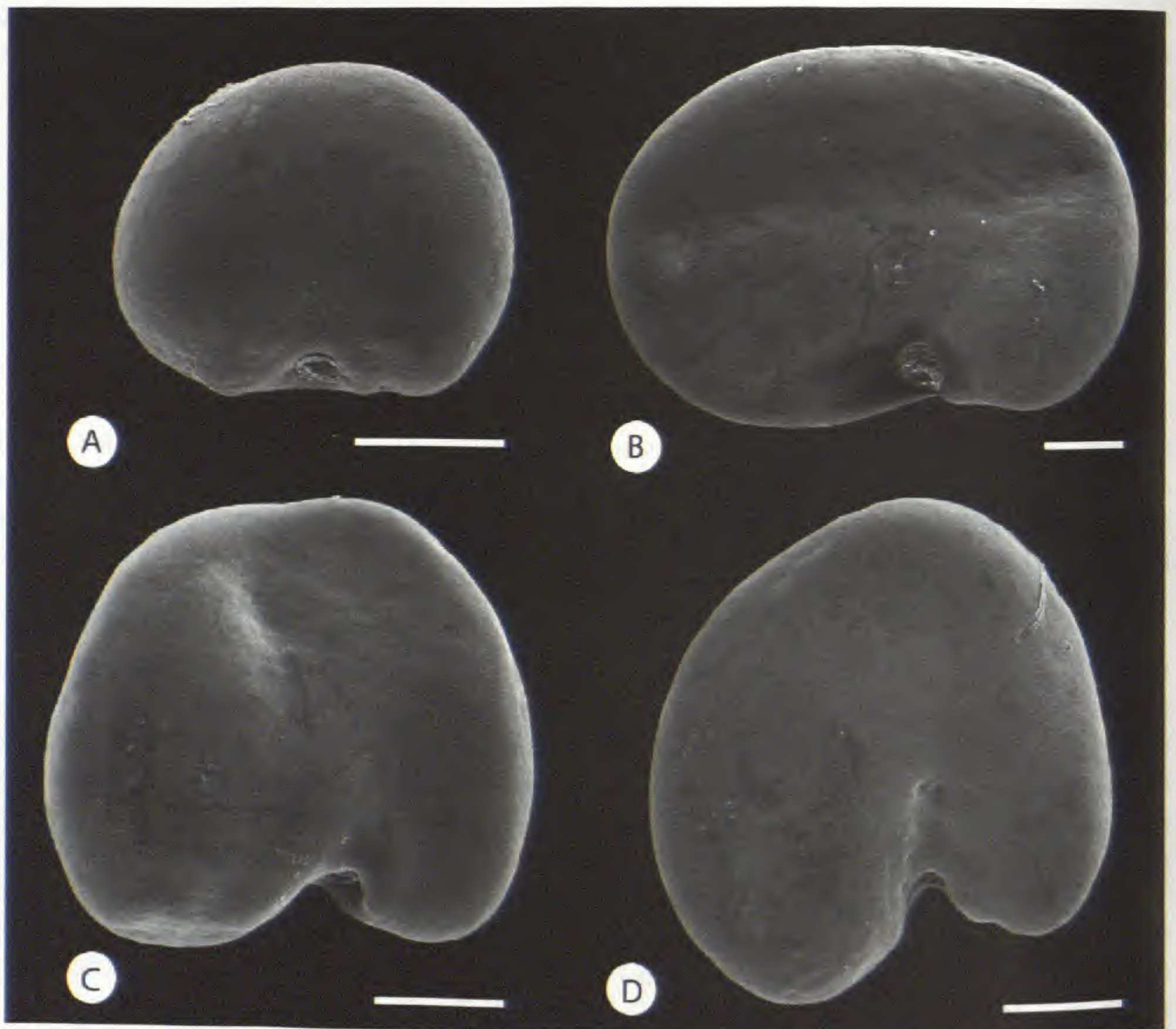


FIG. 1. Seed shapes of *Oxytropis* in Alaska using scanning electron microscopy. A. *Oxytropis deflexa* (Ickert-Bond 1466); B. *Oxytropis tananensis* (Howenstein & Borron 40); C. *Oxytropis borealis* (Parker et al. 13030); D. *Oxytropis campestris* subsp. *gracilis* (Stensvold 5563). A. globose seed. B. ovoid seed. C. reniform seed. D. mitiform seed. Scale bars A-D, 500 μ m.

section *Arctobia* had less variable seed coat patterns as compared to all other sections examined (Table 2, Fig 4). Species classification explained only a minor amount of variation in seed coat type (Table 2). Similarly, length and L:W ratio explained little of the variability of seed coat type (Table 2). Latitude and longitude were the least informative of the independent variables (Tables 1, 2).

DISCUSSION

The current study has revealed several distinct seed shapes, a uniform exotestal anatomy, and three main types of micromorphology of the seed coat (i.e., rugulate, lophate, and foveolate), with most species exhibiting multiple cuticular patterns among different individuals of Alaskan oxytropes. Seeds are typically reniform to mitiform, while infrequently ovoid and globose seeds were found. Anatomically, all seeds examined have the same differentiation into an outer integument with a distinctive combination of sclereid types: an epidermal layer of macroscleroids covering an internal layer of osteoscleroids. Based on micromorphology, we recognized three seed coat types—rugulate, lophate, and foveolate—with additional variations occurring within some of these (i.e., multi-reticulate, and lophate-reticulate). All of the patterns observed in our study were previously noted in seeds of Papilionoideae by Lersten (1981). We note that seed coat micromorphology within

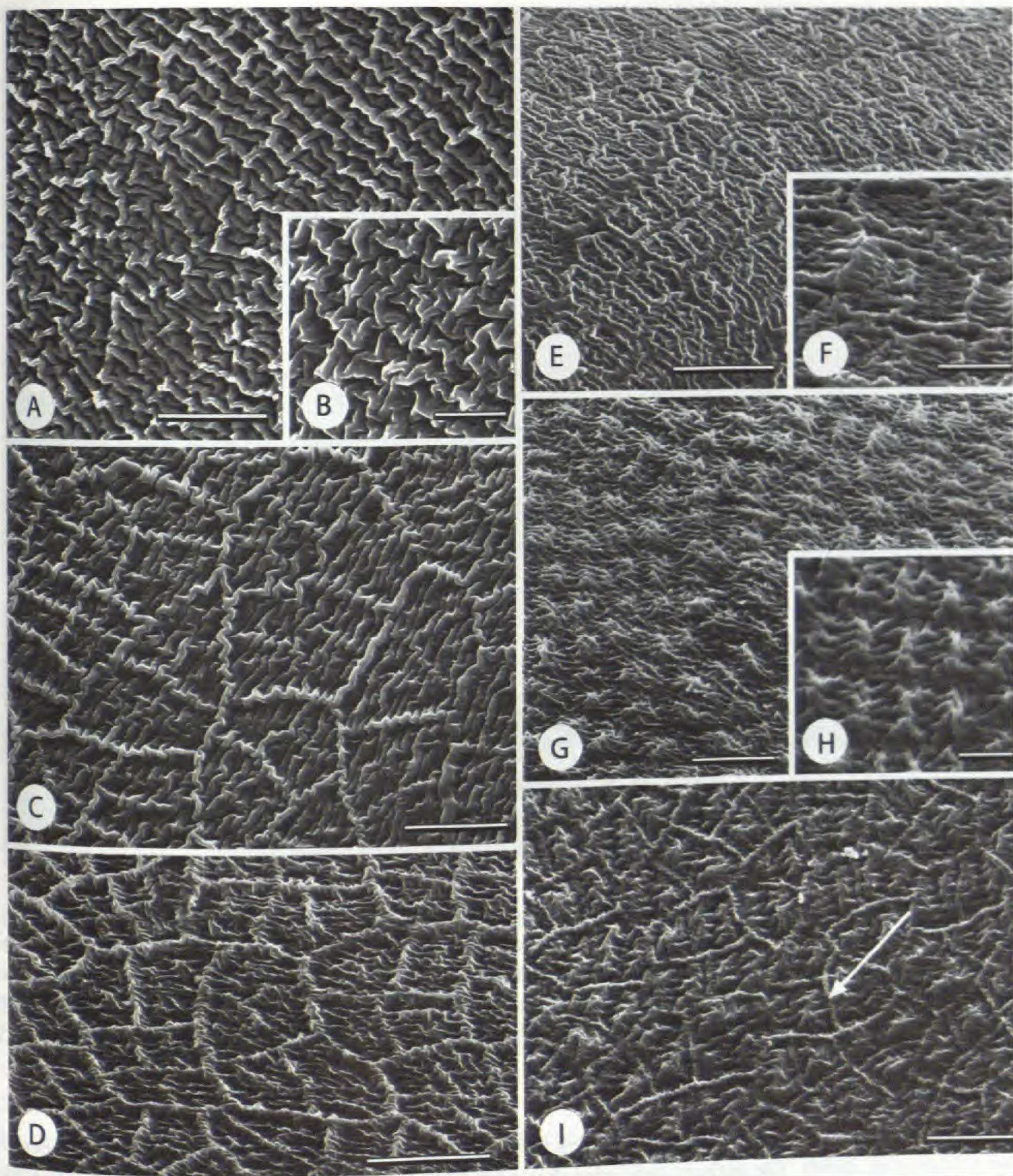


FIG. 2. Seed coat patterns of *Oxytropis* in Alaska using scanning electron microscopy. A–C, *Oxytropis bryophila* (Murray, Yurtsev & Kelso 10658); D, *Oxytropis czukotica* (Koroleva & Petrovsky s.n.); E, *Oxytropis jordalii* (Lipkin & Carlson 03-310) rugulate; F, *Oxytropis viscida* (Raup, Drury, & Raup 13962); G, *Oxytropis arctica* var. *barnebyana* (Jorgensen et al. JJ-97-11-3); H, *Oxytropis koyukensis* (Jorgensen & Batten JJ-99-11-12); I, *Oxytropis kobukensis* (Duffy MD07-123). A, rugulate seed coat pattern. B, details of cuticular folding in rugulate seed coat. C, rugulate-reticulate seed coat. D, multi-reticulate seed coat pattern demonstrating thicker secondary ridge details as compared to C. E, foveolate seed coat. F, foveolate seed coat pattern illustrating details of cuticular folding. G, lophate seed coat. H, details of the cuticular folding and regular spacing of the lophae. I, Lophate-reticulate seed coat showing additional ridges encircling the lophae (arrow). Scale bars A, C–E, G, I, 20 μ m; B, F, H, 10 μ m.

Oxytropis may be entirely of cuticular origin and not a manifestation of the underlying epidermal cells (Fig. 3A–C).

Previous studies investigating *Astragalus* and *Oxytropis* seed coat micromorphology found exotestal characters of limited use. A study that examined 48 species of Turkish *Astragalus* found only two distinct seed coat

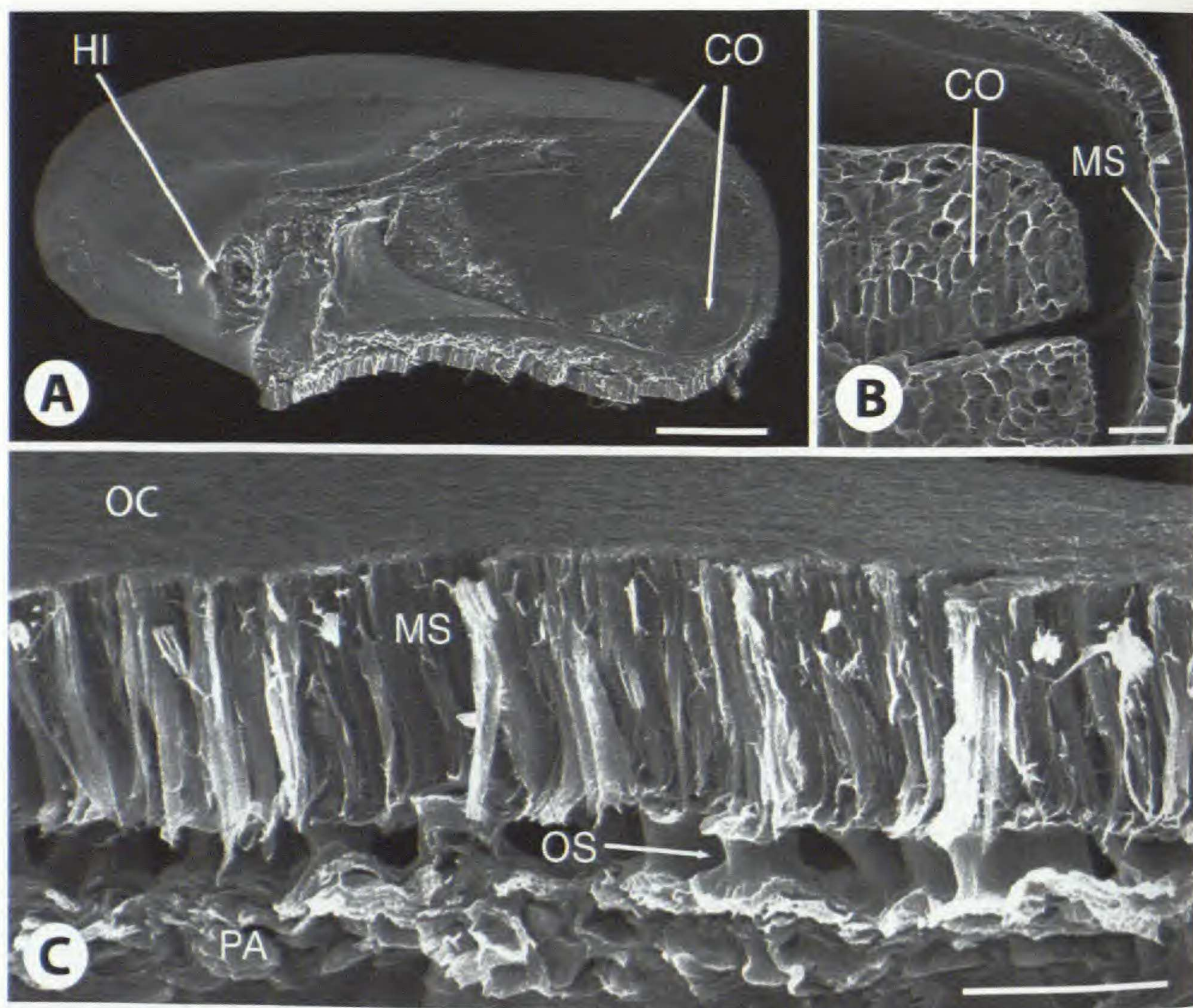


FIG. 3. Seed anatomy of selected species of *Oxytropis* in Alaska using scanning electron microscopy. **A**, *Oxytropis huddelsonii* (Parker et al. 6511); **B**, *Oxytropis tananensis* (Ickert-Bond 1517); **C**, *Oxytropis bryophila* (Ickert-Bond 1526). **A**, Partially sectioned seed showing position of the hilum (HI), and two prominent cotyledons (CO) filling the embryo cavity. **B**, Cross section with detailed view of edge of the seed showing macrosclereids (MS) and cotyledon (CO), outer. **C**, Cross section detailing uniform outer cuticle (OC), macrosclereids (MS) making up the outer epidermis, followed by a row of osteosclereids (OS) forming the hypodermis and tangentially elongated parenchyma cells (PA) of the nucellus. CO = cotyledon, HI = hilum MS = macrosclereids, OC = outer cuticle, OS = osteosclereids, PA = parenchyma. Scale bars A 500 μ m, B 100 μ m, C 50 μ m.

microphological types (rugulate and rugulate-reticulate) and three seed shapes (oblate, suboblate, and peroblate) (Vural et al. 2008). The authors concluded that seed coat patterns at both the species and infrageneric levels were of limited taxonomic utility in *Astragalus* unless supported by macromorphological characters. Similarly, 13 Turkish species of *Oxytropis* were examined and classified as striate-reticulate, psilate-reticulate, reticulate, and striate-rugulate (Erkul and Aytac 2010). Comparison of morphology of these Turkish species with the current study is limited however as these seed coats types (striate-reticulate, psilate-reticulate, reticulate, and striate-rugulate) are not well defined in the study (Erkul and Aytac 2010). The pioneering work of testal topography examination by Lersten in 1981 revealed tribal associations in Leguminosae subfamily Papilionoideae, specifically with Viciaeae, Trifolieae, and Cicerae.

The multinomial logistic regression revealed species delimitation (independent variable) to describe the least amount of seed coat variation (dependent variable), along with latitude and longitude. These results combined with the intraspecific variability in seed coat patterns observed demonstrate that seed coat types cannot be used to discriminate species of Alaskan *Oxytropis* and are not taxonomically useful.

Historically, species delimitation in *Oxytropis* has been controversial, resulting in competing taxonomies

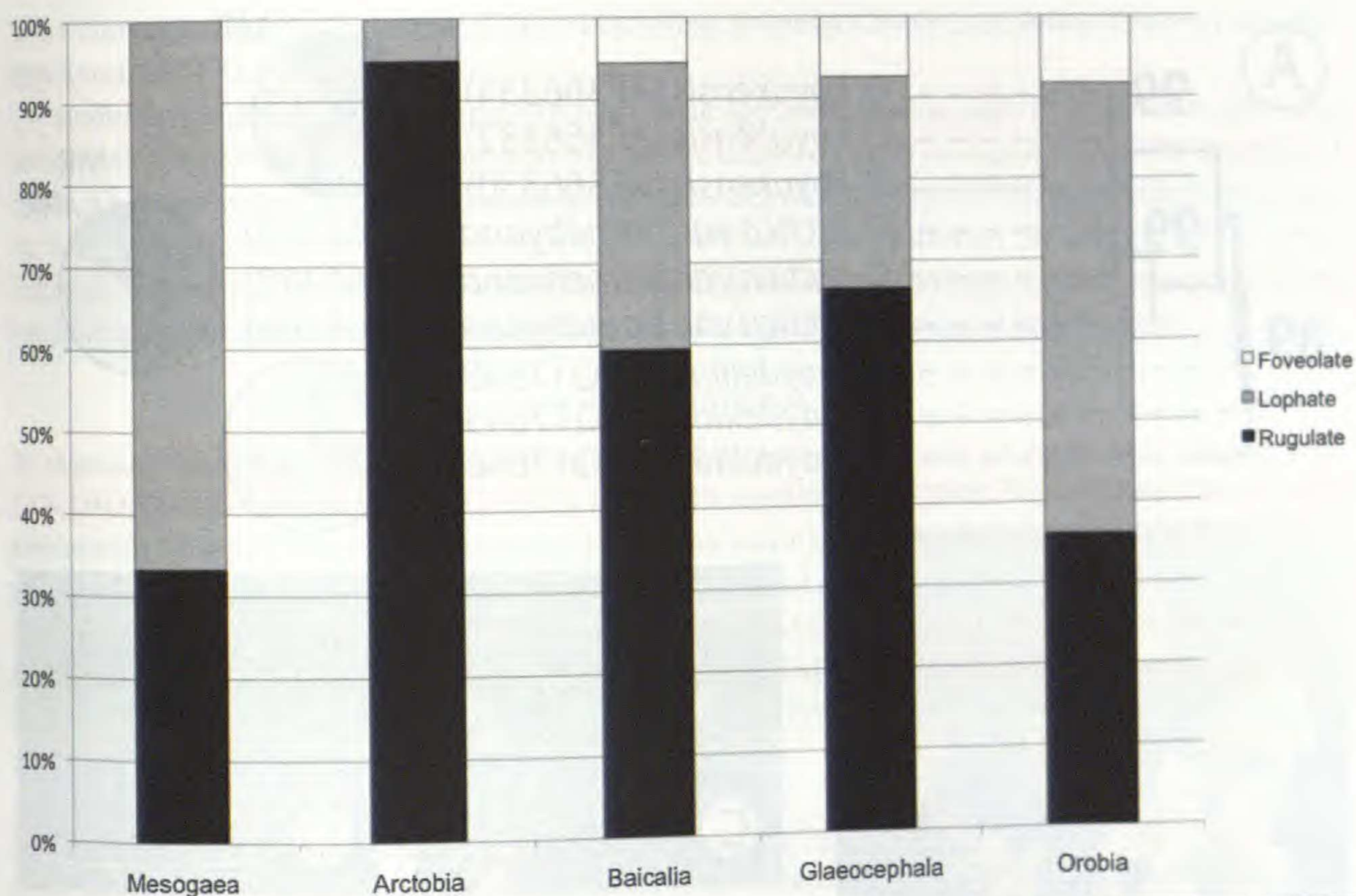


FIG. 4. Frequency of the three main seed coat types found in each of the five sections of *Oxytropis* in Alaska. Primary type percentages are depicted on a gray scale (black = rugulate; gray = lophate; and white = foveolate).

and a plethora of synonyms (reviewed in Welsh 2001) and a number of Alaskan *Oxytropis* taxa are particularly questionable (see Barneby 1952; Yurtsev 1997; Welsh 2001; Jorgensen et al. 2003; Elven & Murray 2011, and if unrecognized, would be taxa of conservation concern (AKNHP 2013). We find no evidence in the seed traits analyzed that support separation of *O. tananensis* from *O. varians/campestris*. *Oxytropis tananensis* has been described as a distinct taxon by Yurtsev in 1993 based on the unique presence of semiverticillate leaflets, whereas Elven and Murray (2011) sees it as part of the natural variation of *O. varians*. Welsh (2001) also synonymized *O. tananensis* with his *O. campestris* var. *varians*. Similarly, there are no seed traits that support separation of the white-flowered plants of *O. arctica* from western Alaska (*O. arctica* var. *barnebyana*, Fig. 5) from the red/blue-flowered *O. arctica* s. str. plants of the Canadian Arctic Archipelago and surroundings (Elven & Murray 2011). We stress, however, that absence of diagnostic seed characters at the species and subspecific-level does not in itself indicate a lack of taxonomic validity of these taxa.

Despite the lack of taxonomic utility at the species level, we observed some trends in frequency of seed coat types at higher infrageneric ranks. Seed coat type and seed shape were distinctive at the sectional level for sections *Arctobia* and *Mesogaea*. Seed coat patterns were most conserved in section *Arctobia* with 97% of the taxa examined being strictly rugulate. Greater variability was observed in the Alaskan members of sections *Orobia*, *Baicalia*, and *Glaeocephala*. Taxa examined from these sections all showed high intraspecific variability in seed coat types.

Despite the variability of seed shapes within sections in Alaskan *Oxytropis*, even within individual species, *Oxytropis deflexa* of subgenus *Phacoxytropis* sect. *Mesogaea* is distinct by having exclusively globose seeds, which range from 1 to 1.5 mm in length and 1.2 to 1.6 mm in width (Table 1; Fig. 1) as compared to seeds examined from other subgenera and sections, which are generally larger and reniform (L = 0.92 to 2.45 mm, W = 1.25 to 2.72 mm, Table 1; Fig. 1). Subgenus *Phacoxytropis* of Bunge (1874) was adopted by Barneby (1952) as well as Yurtsev (1997) as a distinct lineage within *Oxytropis* based on a number of vegetative and reproductive

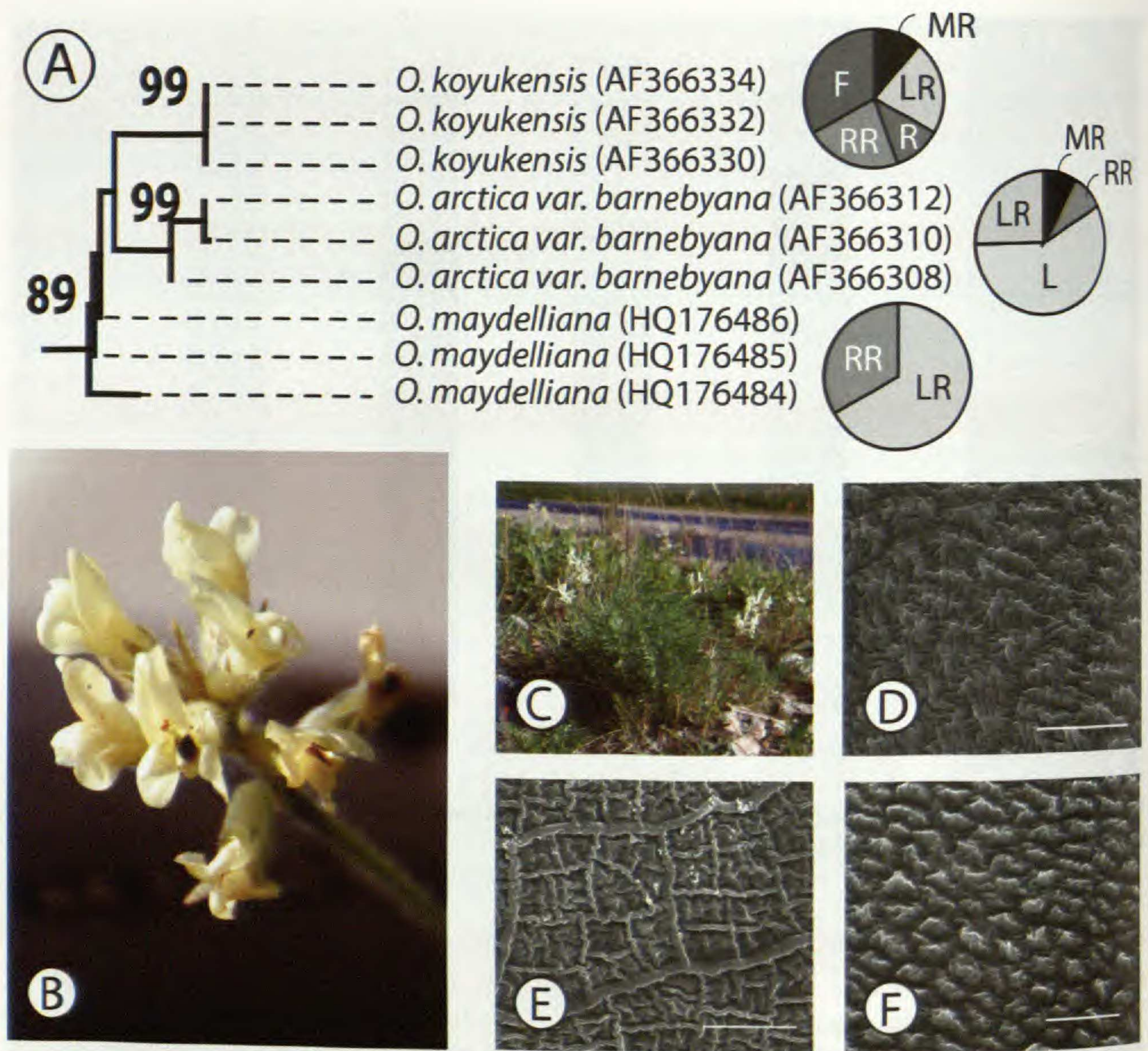


FIG. 5. Intraspecific variation of seed coat patterns in selected *Oxytropis* species from section *Orobia* in Alaska. **A**. Three species from *Oxytropis* section *Orobia* have been shown to form a well supported clade based on molecular data by Archambault and Stromvik (2012). Clade redrawn. Frequency pie graphs are shown next to the taxa at right. Node support (Bayesian posterior probability) is indicated above nodes. Seed coat types are F = foliolate, L = lophate, LR = lophate-reticulate, MR = multi-reticulate, R = reticulate, RR = Rugulate-reticulate. **B**–**F** *Oxytropis arctica* var. *barnebyana*. **B**. Close-up of flowers with distinctive purple tinge at the keel. **C**. Habit on the Seward Peninsula, western Alaska. **D**. Reticulate seed coat pattern. **E**. Rugulate-reticulate seed coat pattern. **F**. Lophate seed coat pattern. Scale bars **D**–**F** 20 μ m.

characters. Molecular evidence strongly support section *Mesogaea* as being an ancestral lineage of *Oxytropis* (Archambault & Stromvik 2012). In addition, *matK* sequence data for 637 legume taxa including seven species of *Oxytropis*, *O. deflexa* was shown to be the earliest diverging branch (unpublished data, Martin F. Wojciechowski, Arizona State University, Tempe, Arizona). However, additional samples of Asiatic members in subgenus *Phacoxytropis* are needed to test whether small globose seeds represent the plesiomorphic seed shape and that reniform seeds represent the derived (apomorphic) condition in *Oxytropis*.

It is crucial to continue reporting detailed observations on morphological diversification as they reveal patterns of evolution in the genus *Oxytropis*, particularly since arctic members have been reported to be the result of recent rapid radiations and hybridization involving polyploidy (Jorgensen et al. 2003; Archambault and Stromvik 2012; Artyukova & Kozyrenko 2012). It is possible that the lack of consistent seed morphology within species is due to past introgression and more current hybridization. Similar rapid colonization events

have occurred in a number of other arctic genera including, *Artemisia*, *Cassiope*, and *Rubus* (Eidesen et al. 2007; Ehrich et al. 2008; Tkach et al. 2008).

Studies investigating the importance of ecology in the speciation process might be particularly promising in *Oxytropis*, where sympatric species are documented to inhabit different ecological niches. For example, *O. czukotica* is an acidophilous species while *O. gorodkovii* is calcicolous (Yurtsev 1999). Also evidence is mounting that populations adapt to similar environments via different genetic pathways (Steiner et al. 2009) further confounding the issue. Taxonomic resolution in a complex genus such as *Oxytropis* will only be achieved using a multi-level approach that integrates phylogenetic, morphological, and ecological investigations.

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